Sylvilagus floridanus.
By Joseph A. Chapman, J. Gregory Hockman, and Magaly M. Ojeda C.

Sylvilagus floridanus (J. A. Allen)
Eastern Cottontail

Lepus sylvaticus Bachman (1837:403). No type or type locality. Name given to the "common gray rabbit" of eastern United States. Name preoccupied by *Lepus borealis sylvaticus* Nilsson, 1832, from Sweden.

Lepus orizabae Merriam (1893:143). Type from Mt. Orizaba, 9500 ft., Puebla, Mexico.

Lepus nigronuchalis Hartert (1894:40). Type from Aruba Island, Netherlands, off the coast of Venezuela near the Paraguana Peninsula.

Lepus cumanicus Thomas (1897:552). Type from Cumana, Sucre Prov., Venezuela.

Lepus margaritae Miller (1898:97). Type from Margarita Island, Venezuela.

Lepus (Sylvilagus) superciliaris J. A. Allen (1899a:196). Type from Bonda, near Santa Marta, Magdalena Prov., Colombia.

Sylvilagus orinoci Thomas (1900:356). Type from Maipures, upper Rio Orinoco, Vichada Prov., Colombia.

Lepus simplicicanus Miller (1902:81). Type from Brownsville, Texas.

Lepus (Sylvilagus) durangae J. A. Allen (1903:609). Type from Rancho Bailon, northwestern Durango, Mexico.

Lepus (Sylvilagus) russatus J. A. Allen (1904:31). Type from Pasa Nueva, southern Veracruz, Mexico.

Sylvilagus cognatus Nelson (1907:82). Type from [Tajique] near summit of Manzano Mountains, 10,000 ft., New Mexico.

Sylvilagus avius Osgood (1910:29). Type from Testigo Grande, Islas de los Testigos, Venezuela.

Sylvilagus cumanicus Allen (1911:249). Type from near Maracaibo, Lake Maracaibo, northern Zulia, Venezuela.

Sylvilagus valenciae Thomas (1914:413). Type from El Trompillo, southeast of Lake Valencia, Carabobo Prov., 1300 ft., Venezuela.

Sylvilagus boylei J. A. Allen (1916:84). Type from La Playa, northwest of Barranquilla, Colombia.

Sylvilagus purgatus Thomas (1920:32). Type from Purificacion, Rio Magdalena, Tolima Prov., 292 m, Colombia.

CONTEXT AND CONTENT. Order Lagomorpha, Family Leporidae, Genus *Sylvilagus*, Subgenus *Sylvilagus*. There are about 14 recognized living species in the genus and 35 recognized subspecies of *S. floridanus* (Hall, 1951; Hall and Kelson, 1959; Hershkovitz, 1950; Hoffmeister and Lee, 1963) as follows:

S. f. alacer (Bangs, 1896:136). Type from Stilwell, Indian Territory [Boston Mountains, Adair County, Oklahoma].

S. f. ammophilus A. H. Howell (1939:365). Type from "Oak Lodge," on Peninsula opposite Micco, Florida.

S. f. avius Osgood (1910:29), see above.

S. f. aztecus (J. A. Allen, 1890a:188). Type from Tehuantepec [City], Oaxaca, Mexico.

S. f. chapmani (J. A. Allen, 1899b: 12). Type from Corpus Christi, Nueces County, Texas (*caniclunis* Miller and *simplicicanus* Miller are synonyms).

S. f. chiapensis (Nelson, 1904:106). Type from San Cristobal, Chiapas, Mexico.

S. f. cognatus Nelson (1907:82), see above.

S. f. connectens (Nelson 1904:105). Type from Chichicaxtle, central Veracruz, Mexico.

S. f. continentis Osgood (1912:57). Type from near Maracaibo, Lake Maracaibo, northern Zulia, Venezuela.

S. f. costaricensis Harris (1933:3). Type from Hacienda Santa Maria, Province of Guanacaste, 3200 ft., Costa Rica.

S. f. cumanicus (Thomas 1897:552), see above (*margaritae* Thomas and *supercilianis* Thomas are synonyms).

S. f. floridanus (J. A. Allen 1890b:160). Type from Sebastian River, Brevard County, Florida.

S. f. hesperius Hoffmeister and Lee (1963:140). Type from 5.25 mi. SE Kingman, Hualpai Mountains, Mohave County, Arizona.

S. f. hitchensi Mearns (1911:227). Type from Smiths Island, Northampton County, Virginia.

S. f. holzneri (Mearns, 1896:554). Type from Douglas spruce zone, near summit of Huachuca Mountains [Cochise County], Arizona (*rigidus* Mearns and *durangae* J. A. Allen are synonyms).

S. f. hondurensis Goldman (1932:122). Type from Monte Redondo, approximately 30 mi. NW Tegucigalpa, 5100 ft., Honduras.

S. f. llanensis Blair (1938:1). Type from old "F" Ranch headquarters, Quitaque, Briscoe County, Texas.

S. f. mallurus (Thomas, 1898:320). Type from Raleigh, Wake County, North Carolina (*sylvaticus* Bachman is a synonym).

S. f. margaritae (Miller, 1898:97), see above.

S. f. mearnsi (J. A. Allen, 1894:171). Type from Fort Snelling, Hennepin County, Minnesota.

S. f. nelsoni Baker (1955:611). Type from 22 mi. S, 5 mi. W Ocampo, 5925 ft., Coahuila.

S. f. nigronuchalis (Hartert, 1894:40), see above.

S. f. orinoci Thomas (1900:356), see above.

S. f. orizabae (Merriam, 1893:143). Type from Mt. Orizaba, 9500 ft., Puebla, Mexico (*persultator* Elliot is a synonym).

S. f. paulsoni Schwartz (1956:147). Type from 6 mi. N Homestead, Dade County, Florida.

S. f. purgatus Thomas (1920:32), see above.

S. f. restrictus Nelson (1907:82). Type from Zapotlan, Jalisco, Mexico.

S. f. robustus (Bailey, 1905:159). Type from 6000 ft. Davis Mountains, Jeff Davis County, Texas.

S. f. russatus (J. A. Allen, 1904:31), see above.

S. f. similis Nelson (1907:82). Type from Valentine [Cherry Co.], Nebraska.

S. f. subcinctus (Miller, 1899:386). Type from Hacienda El Molino, near Negrete, Michoacan.

S. f. superciliaris (Allen, 1899a:196), see above (*boylei* Allen is a synonym).

S. f. valenciae Thomas (1914:413), see above.

S. f. yucatanicus (Miller, 1899:384). Type from Merida, Yucatan.

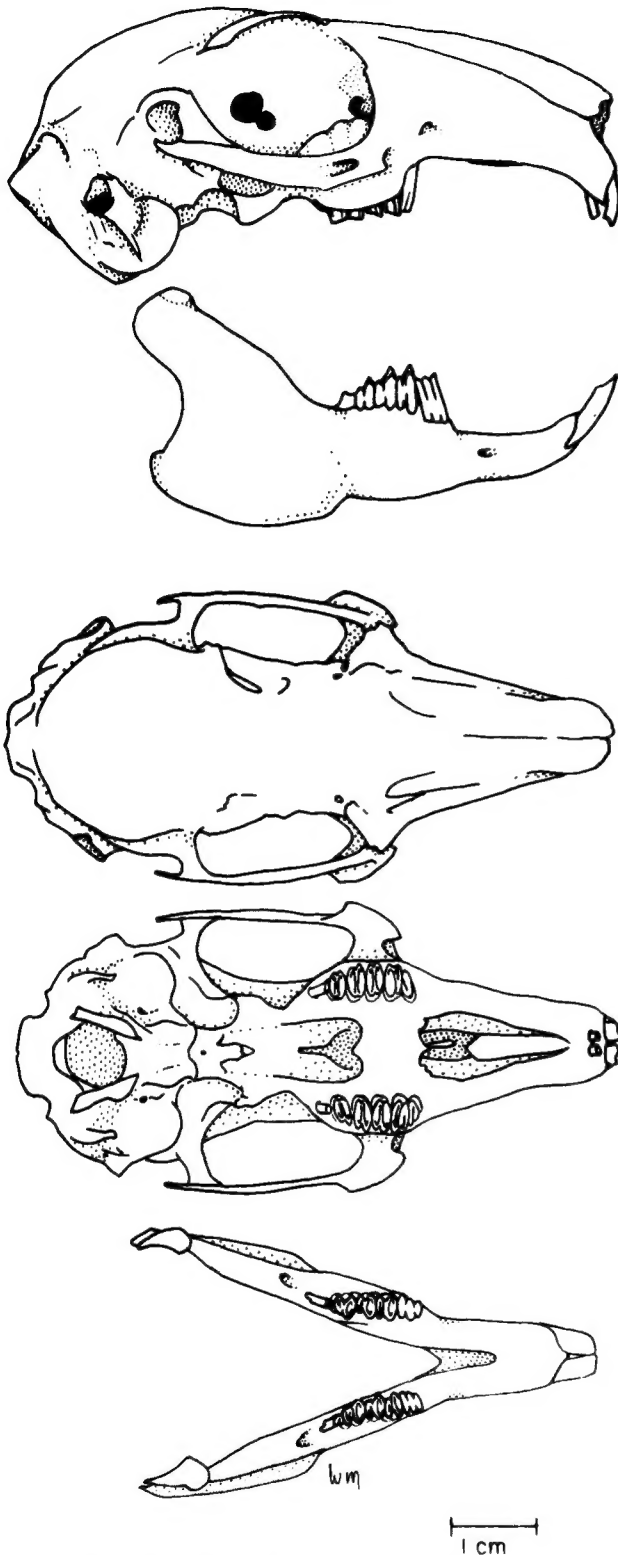FIGURE 1. *Sylvilagus floridanus*. Photo by Leonard Lee Rue II.

thickened, posterior extension of the supraorbital process of the frontal. Because this species has the widest distribution of any *Sylvilagus*, characteristics which are diagnostic for the species vary according to locality. However, in local areas it is generally easy to distinguish *S. floridanus* from other sympatric rabbits. The only exception is the separation of *S. floridanus* and *S. transitionalis* on the basis of pelage where the two occur sympatrically along the Appalachians and in New England. These two rabbits are easily identified on the basis of cranial characters (for a detailed description of the differences between these species and photographic illustrations see Chapman, 1975). The skull is illustrated in Fig. 2.

GENERAL CHARACTERS. Descriptions are given in Nelson (1909), Hall (1951), and Hall and Kelson (1959). Females are about 1% larger than males (Chapman and Morgan, 1973). The dental formula is i 2/1, p 3/2, m 3/3, total 28.

Some average external measurements (in mm) for 33 to 35 *S. floridanus* males, with ranges in parentheses, are: total length, 427.0 (395 to 456); length of tail, 44.9 (25 to 54); length of hind foot, 95.4 (90 to 105); length of ear (from notch), 61.5 (55 to 67). Corresponding measurements for 41 to 42 females are: 433.2 (400 to 477); 44.8 (28 to 61); 95.4 (90 to 104); 61.1 (56 to 67) (Chapman and Morgan, 1973). Weight of 64 adult males averaged 1,134.4 g (range, 801 to 1,411), and 36 adult females averaged 1,244.0 (842 to 1,533) (Chapman and Morgan, 1973).

Mean cranial measurements (in mm ± SD) of 59 to 78 adult *S. floridanus* from Maryland are: basilar length, 56.17 ± 1.98; zygomatic breadth, 36.30 ± 1.10; postorbital constriction, 12.24 ± 0.87; length of nasals, 31.51 ± 1.43; width of nasals, 15.00 ± 0.89; length of maxillary toothrow, 13.95 ± 0.58; diameter of external auditory meatus, 4.11 ± 0.19; breadth of brain case, 23.62 ± 0.68; length of palatal bridge, 6.33 ± 0.62; depth of rostrum, 14.66 ± 0.67; parietal breadth, 24.24 ± 0.87; length of bulla, 10.22 ± 0.46 (Chapman and Morgan, 1973). Additional measurements of North and Central American forms may be found in Nelson (1909), Hall (1951), Hall and Kelson (1959), and Chapman and Morgan (1973). Measurements of South American forms may be found in Hummelinck (1940), Hershkovitz (1950), and Bracamonte (1972).

DISTRIBUTION. The eastern cottontail has the widest distribution of any species of *Sylvilagus* (Hall, 1951; Hershkovitz, 1950). It is unique among the rabbits of the world in that it inhabits diverse areas, occurring over broad geographic provinces from southern Canada into Central and northwestern South America, including some islands north of Venezuela (Figs. 3 and 4). This cottontail is generally thought of as a mammal of farmlands, fields, and hedge rows; however, historically it occurred in natural glades and woodlands, deserts, swamps, prairies, hardwood forests, rain forests, and boreal forests. The species has been widely introduced and populations are now established in Oregon (Graf, 1955) and Washington (Dalquest, 1941).

The eastern cottontail occurs sympatrically with many other rabbits. Its range overlaps that of six species of *Sylvilagus* and six species of *Lepus*. No other species occurs sympatrically with this many other leporids. Recent studies have shown that widely separated populations of *S. floridanus* have different genetic compositions which may account for the species' ability to occupy diverse habitats (Chapman and Morgan, 1973).

FOSSIL RECORDS. The fossil history of *S. floridanus* is well documented from Pleistocene deposits. Specimens of *Sylvilagus* from the Pleistocene of Schulze Cave, Edwards County, Texas (Dalquest et al., 1969), the Duck Creek local fauna of Kansas (McMullen, 1978), the Isleta Caves fauna, New Mexico (Harris and Findley, 1964), and the Melbourne fauna, Florida (Gazin, 1950) have been referred to *S. floridanus*. The early Holocene record of *S. floridanus* is well documented (Guilday and Bender, 1958; Guilday and Parmalee, 1965; Gilmore, 1946; Parmalee, 1962). Fossil remains of *S. floridanus* from the late Irvingtonian to Recent have been reported in Arkansas, Illinois, Maryland, Wisconsin, Nebraska, Pennsylvania and Tennessee (Kurtén and Anderson, in press).

FORM AND FUNCTION. Adult eastern cottontails undergo two distinct molts per year (Negus, 1959). The spring molt from winter to summer pelage is a gradual process taking place from March to August (Dalke, 1942). The fall molt begins in late September; full winter pelage is attained by the first week in November (Negus, 1959). Reproductive activity is related to the onset of the adult molt (Negus, 1959).

FIGURE 2. Skull and mandible of *Sylvilagus floridanus* (male [AEL-940] from St. Clements Island, Potomac River, St. Marys County, Maryland). Drawing by Wilma Martin. Above, lateral view of cranium and mandible; middle dorsal view; below, ventral view of cranium and dorsal view of mandible.

DIAGNOSIS. This is a large cottontail (Fig. 1). The pelage is long and dense, brownish to greyish on the upper parts and white on the underside of the body and tail. The South American forms have a nuchal patch which varies from yellowish-brown to black in the different subspecies. The skull has a transversely
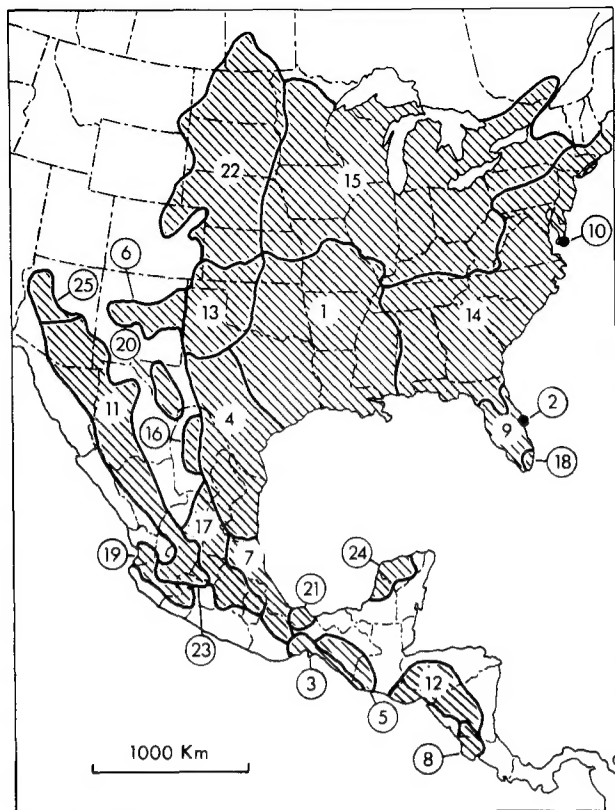
FIGURE 3. Distribution of *Sylvilagus floridanus* in North and Central America: 1, *S. f. alacer*; 2, *S. f. ammophilus*; 3, *S. f. aztecus*; 4, *S. f. chapmani*; 5, *S. f. chiapensis*; 6, *S. f. cognatus*; 7, *S. f. connectens*; 8, *S. f. costaricensis*; 9, *S. f. floridanus*; 10, *S. f. hitchensi*; 11, *S. f. holzneri*; 12, *S. f. hondurensis*; 13, *S. f. llanensis*; 14, *S. f. mallurus*; 15, *S. f. mearnsi*; 16, *S. f. nelsoni*; 17, *S. f. orizabae*; 18, *S. f. paulsoni*; 19, *S. f. restrictus*; 20, *S. f. robustus*; 21, *S. f. russatus*; 22, *S. f. similis*; 23, *S. f. subcinctus*; 24, *S. f. yucatanicus*; 25, *S. f. hesperius*. Adapted from Hall and Kelson (1959); Hall (1951); Hoffmeister and Lee (1963); Anderson (1972); Armstrong (1971), and Findley et al. (1975).

FIGURE 4. Distribution of *S. floridanus* in South America: 26, *S. f. avius*; 27, *S. f. continentis*; 28, *S. f. cumanicus*; 29, *S. f. margaritae*; 30, *S. f. nigronuchalis*; 31, *S. f. orinoci*; 32, *S. f. purgatus*; 33, *S. f. superciliaris*; 34, *S. f. valenciae*. Adapted from Cabrera (1961); Gimenez-Bracamonte (1972); Hershkovitz (1950); Hummelinck (1940); and Musso (1962).

A partial *bursa ovarica* with a very large orifice is found medial to the ovary. Ovaries are found in the lumbar region and are fusiform in shape. Ripe graffian follicles remain small and maintain a medium size antrum with several radiating trabeculae. A thick thecal gland is present within the generally smooth surfaced ovary (Mossman and Duke, 1973).

Chapman et al. (1977) found *S. floridanus* was in its best condition in spring according to a weight-length condition index (K). Adrenal index curves showed that eastern cottontails exhibited highest stress during the winter and second highest stress during the breeding season (spring). Body fat index for *S. floridanus* peaked in fall, adrenal index peaked in winter and condition peaked in spring. Females remain in better condition during the breeding season than males according to the three physiological indices. Males have significantly higher mean adrenal indices year-round than females.

ONTOGENY AND REPRODUCTION. In Maryland, the mean ovulation rate was 5.75, with 6% of the ova being resorbed and approximately 7% failing to implant or being resorbed prior to becoming visible (Chapman et al., 1977). The ovulation rate of Missouri cottontails was 4.18, with a partial litter resorption rate between 5% and 12% (Conaway and Wight, 1962; Evans et al., 1965). Pelton (1969) reported 3.3% of the fetuses were resorbed in cottontails from Georgia. Ovulation rates in Texas varied from 1.47 to 4.09 (Bothma and Teer, 1977).

The mean gestation period is 28 to 29 days with a range from 25 to 35 days (Dice, 1929; Dalke, 1942; Bruna, 1952; Evans, 1962; Marsden and Conaway, 1963).

Bruna (1952) reported the number of litters per year was three or four. The average number of litters produced in Maryland
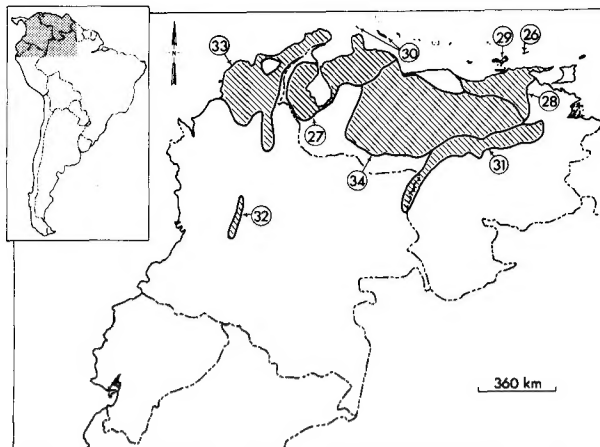
was 4.6 per female per year (Chapman et al., 1977). Litter numbers of five to seven per year were reported by Sheffer (1957), Conaway et al. (1963), Evans et al. (1965) and Tretheway and Verts (1971). The litter size of the first pregnancy of the year is influenced by age and, or, previous reproductive experience (Lord, 1961a; Conaway and Wight, 1962). The size of the first litter increases when there is a delay in the onset of reproduction (Conaway and Wight, 1962).

The mean size of the first litter varies from about three in Alabama to five or greater in Maryland and North Dakota (Chapman et al., 1977; Chapman and Morgan, 1974; Conaway et al., 1974; Hill, 1972). Conaway et al. (1974) found mean annual litter sizes to be correlated with latitude and with other factors such as conception dates, body weight, elevation and on a single occasion, longitude. In the United States, mean annual litter size varies from 3.1 in Georgia to 5.6 in Illinois (Ecke, 1955; Pelton and Jenkins, 1971). As a rule South American forms have 2 young per litter, rarely 1 or 3 (Hummelinck, 1940).

Ecke (1955) gave the following description and average measurements of neonates: weight, 35 to 45 g; total length, 90 to 110 mm; and hind foot, 21 to 23 mm. Young at birth were covered with fine hair, their eyes were tightly closed, and their legs were developed enough to enable them to crawl into the nest. Their eyes opened on day 4 or 5 and young were able to leave the nest on days 14 to 16 after birth. Nestlings from Kentucky opened their eyes at days 7 to 8 and were able to move out of the nest at day 14 (Bruna, 1952). Nestling rabbits in southern Texas opened their eyes between days 6 and 7 and moved away from the nest at day 12 (Bothma and Teer, 1977).

Initial reproductive activity occurs later at higher elevations and at higher latitudes (Conaway et al., 1974). In Alabama the breeding season begins in the first week of January (Barkalow, 1962) and continues to the last week in March in southern Wisconsin (Rongstad, 1966). The breeding season in Connecticut lasts from mid-March to mid-September (Dalke, 1942), in New York, from February through September (Schierbaum, 1967), and in western Maryland from late February through August (Chapman et al., 1977). In the southern latitudes the breeding seasons are of longer duration. In Georgia, cottontails have a nine-month breeding season (Pelton and Provost, 1972) while in south Texas they breed year-round (Bothma and Teer, 1977). An introduced population in western Oregon began to breed in late January and ceased in early September (Trethewey and Verts, 1971). The onset of breeding varies between different populations and within the same population from year to year (Conaway and Wight, 1962; Hill, 1966). Hill (1966) suggested that temperature, rather than diet, is the primary factor controlling the onset of breeding. Many studies have correlated severe weather with delays in the onset of the breeding season (Hamilton, 1940; Wight and Conaway, 1961; Conaway and Wight, 1962). Ecke (1955) believed that the limits of the breeding season are closely related to the availability of succulent vegetation. Change in photoperiod is an important factor in regulating cottontail breeding (Bissonnette and Csech,

1939). The major environmental factors controlling breeding activity in south Texas are temperature and rainfall. Rainfall affects the amount of succulent vegetation available (Bothma and Teer, 1977).

Many studies have reported breeding in young-of-the-year juveniles: Negus (1959) found that 50% of juveniles bred; Stevens (1962), Lord (1963), and Trethewey and Verts (1971) observed that 44%, 27%, and 52% of juveniles bred, respectively. Other investigations found that breeding of juveniles was substantially lower than that of adults in terms of total productivity. Bothma and Teer (1977) reported 7.6% of all pregnant females were young-of-the-year. Juvenile females accounted for 3.9% of the pregnancies and only 2.7% of total ovulations in Maryland (Chapman et al., 1977). Pelton (1969) reported that 4.4% of the total young-of-the-year showed indications of breeding.

Annual production in Missouri was 35 young per adult female (Conaway et al., 1963). Pelton and Jenkins (1971) reported a lower potential productivity by Georgia cottontails (15 to 21 young per adult female per year) than cottontails from Missouri. Adult females in Oregon produced 24 to 35 young in five to seven litters (Tretheway and Verts, 1971). Bothma and Teer (1977) calculated that the potential productivity of adult females was 9.4 young per female per year. Chapman et al. (1977) estimated 23.9 young were produced per breeding female per year in an average of 4.6 litters. In Texas, potential productivity of juvenile females was found to be 6.2 young per female per year (Bothma and Teer, 1977). These authors concluded that the juvenile contribution to the production of young was mainly dependent upon their proportion in the overall female population.

Conaway et al. (1963) found synchronized breeding behavior. Photoperiod is thought to regulate synchronization of the initial pre-estrus stage on all populations over a wide geographic area (Conaway and Wight, 1962). A cycle of recurring pre-estrus has been postulated as explaining synchronous conceptions of approximately fourteen-day intervals (Conaway and Wight, 1962; Evans et al., 1965). Marsden and Conaway (1963) suggested a 7-day behavioral rhythm during the onset of breeding and first pregnancy. This 7-day rhythm is apparently absent in postpartum breeding cycles. Cottontails from Georgia and Missouri exhibited synchrony throughout the breeding season (Wight and Conaway, 1962; Conaway et al., 1963; Pelton and Provost, 1972). Once breeding begins, synchronous peaks of conception are determined by the length of gestation (Conaway and Wight, 1962; Evans, 1962).

Trent and Rongstad (1974) reported mean annual survival rates for adults of 0.20. Average life span in the wild is 15 months (Bruna, 1952). Lord (1963) stated that the potential life span of cottontails was at least 10 years. Salo (1965) concluded that females have greater longevity than males.

ECOLOGY. *Sylvilagus floridanus* is widely distributed throughout various habitats within its range. No single habitat type may be classed as preferred cover. Habitat preferences vary from season to season, between latitudes and regions, and with differing behavioral activities.

Nests are slanting holes in the ground with average measurements of: length, 180 mm; width, 126 mm; depth, 119 mm (Friley, 1955). In Texas, five nests averaged 125 mm long, 104 mm wide, and 91 mm deep (Bothma and Teer, 1977). Casteel (1966) found the average measurements from 21 nests to be 102 mm deep, 121 mm wide, and 146 mm long. There is no relationship between size of the nest and size of litter (Bothma and Teer, 1977). Nest holes in farming areas in southern Michigan contained an outer lining of grass or herbaceous stems covering all sides and a heavy, inner layer of belly or side fur from the female (Friley, 1955). Nests from Illinois were lined first with leaves, then with an inner lining of fur plucked from the female (Ecke, 1955). Casteel (1966) determined that residual vegetative cover was the preferred nest material, especially grass stems when available. Casteel (1966) found that females pulled fur from almost every part of their body, except the abdomen, for nest construction.

In Connecticut, brushpiles were apparently preferred as shelter and resting cover. Where brushpiles were absent, cleared spots or forms under herbaceous and shrubby vegetation were used as hiding and resting places. Brushpiles in cut-over woodlands provide winter shelter and an adequate supply of winter food consisting of stump sprouts and exposed shrubby and herbaceous vegetation (Dalke, 1942).

In southern Michigan farming areas, forms composed of native herbaceous vegetation, with dense herbaceous cover on all sides, were preferred. Grass was the basic construction material.

Spring forms were constructed of brush and briars and winter forms of herbaceous vegetation (Friley, 1955).

Bruna (1952) stated that use of cover is probably determined by availability and location, rather than any individual preference. Broomsedge and woods in Kentucky were utilized frequently throughout all seasons (Bruna, 1952).

Smith (1950) concluded that the habitat requirements for cottontails in the Hudson Valley of New York include grasslands, hedgerows, areas of low, dense brush, and dens for escape. Old field situations were also reported as highly-preferred habitat by Friley (1955), Heard (1962), and Nugent (1968). Woodchuck holes provide the best dens for escape cover and shelter (Smith, 1950).

Cottontail habitat has been improved by interspersion of old fields and briar thickets, creation of edge and by establishment of open food plots or by breaking up large, continuous parcels of monotypic habitat (Smith, 1950; Bruna, 1952; Friley, 1955; Heard, 1962; and Nugent, 1968). Burning followed by grazing was found to be destructive to habitat quality (Heard, 1962).

South American forms inhabit arid and semi-arid regions of Colombia, Venezuela, and some adjacent islands, from sea level to 1000 m (Hershkovitz, 1950). Handley (1976) found that in South America, the species composition of rabbits varied with habitat, with *S. floridanus* accounting for 97% of the rabbits in dry upland habitats, 76% in thorn forest, 20% in savannas and pastures, and 4% in orchards and deciduous forests.

There have been numerous studies of the home range size of the eastern cottontails involving radio-telemetry, trapping and direct observation. In general, yearly mean home ranges for adult males varied from 0.95 ha (2.34 acres) to 2.8 ha. Adult female yearly home range size varied from 0.95 to 1.2 ha (Lord, 1963; Trent and Rongstad, 1974).

Home range size is near the maximum in a rabbit's first winter (Janes, 1959). Home range size and movements of adult rabbits varies by season, sex, and individual (Chapman and Trethewey, 1972a). Trent and Rongstad (1974) reported that home range size of males increased with the onset of sexual activity. Habitat quality and sexual behavior influence the home range size of males during the breeding season. These findings support those of Janes (1959). Home ranges overlap indiscriminately after breeding activity has ended (Trent and Rongstad, 1974). Cottontails do not maintain territories (Allen, 1939; Janes, 1959).

Janes (1959) reported homing ability for two rabbits in Kansas. A male and female were displaced 586.3 m (1800 ft) and 358.3 m (1100 ft) respectively, and were found one month later in their original home ranges. Hill (1967) reported that a female cottontail returned to its original capture site after escaping from an enclosure 3.74 km (2.33 mi) distant.

In southern Wisconsin, fall population densities of rabbits were 8.9/ha (Trent and Rongstad, 1974). The peak density for a small island in Maryland was 10.18/ha (Bittner and Chapman, 1979).

Cottontails feed upon a wide variety of plant species. In New York herbaceous species were chosen during the growing season, and woody species were chosen during the dormant season. Woody plants, in order of importance as food are: apple (*Malus pumila*), staghorn sumac (*Rhus typhina*), red maple (*Acer rubrum*), blackberry (*Rubus allegheniensis*), red raspberry (*R. strigosus*). Herbaceous species of importance are: Kentucky bluegrass (*Poa pratensis*), Canada bluegrass (*P. compressa*), timothy (*Phleum pratense*), quack grass (*Agropyron repens*), orchard grass (*Dactylis glomerata*), red clover (*Trifolium pratense*), and wild carrot (*Daucus carota*). Staghorn sumac was chosen over smooth sumac (Smith, 1950).

In Ohio, herbaceous plants, except when snow covered, comprised almost the entire diet. Bluegrass was the most important all-season food. Orchard grass, timothy, and nodding wildrye (*Elymus canadensis*) are all-season foods of lesser importance. Red clover and Korean lespedeze (*Lespedeza stipulacea*) were utilized seasonally (Dusi, 1952). Young cottontails preferred dandelion (*Taraxacum officinale*) and prickly lettuce (*Lactuca scariola*), but also ate giant ragweed (*Ambrosia trifida*), red clover, Rugel's plantain (*Plantago rugelii*), and curly dock (*Rumex crispus*), also (Bailey and Siglin, 1966).

Dalke and Sime (1941) observed two pronounced feeding periods, the first was 3 to 4 h after sunrise and second was from sunset to 1 h after. Feeding habits varied with changes in seasons and the succession of plants. Spring through October diets consisted of herbaceous plants, mainly clover, timothy and alfalfa. The fall period, November and December, was a transition period from herbaceous to woody plant materials. Winter diets consisted mainly of tree species, including gray birch (*Betula populifolia*), red maple, apple, aspen (*Populus tremuloides*), choke cherry

(*Prunus virginiana*), and wild black cherry (*P. serotina*); and the shrubs and vines, blackberry, dewberry (*Rubus villosus*), willow (*Salix*), black alder (*Ilex verticillata*), male berry (*Lyonia ligustrina*), and highbush blueberry (*Vaccinium corymbosum*).

Coprophagy has been reported for the genus *Sylvilagus* (Hamilton, 1955). Cottontails excrete two types of pellets, hard, brown fecal pellets and soft, greenish food pellets. Digestion has extracted the nutrients from hard pellets, which comprise approximately 60% of the total fecal excretion (Bailey, 1969). According to P. R. Cheeke (pers. comm.) soft pellets are produced in the caecum and provide vitamin B supplementation.

The following ectoparasites were reported from *S. floridanus*: ticks, *Haemaphysalis leporispalustris*, *Dermacentor variabilis*, and *Ixodes dentatus*; fleas, *Ceratophyllus multispinosus*, *Cediopsylla simplex*, *Odontopsyllus multispinosus*, *Hoplopsyllus affinis*, and *Ctenocephalides canis*; botflies, *Cuterebra buccata*, *Haemaphysalis justakochi*, *Amblyomina parvum*, *Amblyomma americana*, *Ornithodoros puertorcencis*, *Ctenophthalmus pseudagyrtes*, and *Neotrombicula whartoni* (Jones et al., 1972; Morgan and Waller, 1940; Stannard and Pietsch, 1958; Heard, 1962; Jacobson and Kirkpatrick, 1974; Jacobson et al., 1978). Internal parasites include: cestodes, *Ctenotaenia ctenoids*, *C. variabilis*, *Mosgovoyia pectinata*, *Multiceps serialis*, *Taenia pisiformis*, *Cittotaenia perplexa*, *C. pectinata*, *Cysticencus dearmasi*, *Hydatigera lyncis*, and *Taenia hydatigena*; trematode, *Hasstilesia tricolor*; nematodes, *Dermatoxy veligera*, *Nematodirus triangularis*, *N. leporis*, *Obeliscoides cuniculi*, *Passalurus ambiguus*, *P. nonanulatus*, *Physaloptera* sp., *Trichostrongylus affinis*, *T. calcaratus*, *Dirofilaria scapiceps*, *Trichuris leporis*, *T. sylvilagi*, *Baylisascaris procyonis*, and *Ascaris columnaris* (Morgan and Waller, 1940; Erickson, 1947; Heard, 1962; Novelsky and Dyer, 1970; Jacobson and Kirkpatrick, 1974; Jacobson et al., 1974; Nettles et al., 1975; Jacobson et al., 1976; Diaz-Ungria, 1973).

Bacterial and viral infections such as tularemia (*Francisella tularensis*), Tyzzer's disease (*Bacillus piliformis*), *Herpesvirus sylvilagus*, and *Staphylococcus* have also been reported for *S. floridanus* (McCoy and Steenbergen, 1969; Pelton and Hubbard, 1969; Ganaway et al., 1976; Lewis and Hinze, 1976).

Jacobson et al. (1978) suggested that the pathologic effects of high infestation of parasites impair cottontail reproduction. Changes in physiologic measurements associated with disease infestations have been reported by Jacobson et al. (1978).

Cottontails are a stable food item of most carnivorous mammals found within the cottontail's range. Mammalian predators include raccoons (*Procyon lotor*), ring-tailed cats (*Bassariscus astutus*), marten (*Martes americana*), fisher (*M. pennanti*), weasels (*Mustela*), red fox (*Canis vulpes*), gray fox (*Canis cinereoargenteus*), coyotes (*Canis latrans*), bobcats (*Felis rufus*), and feral cats (*Felis catus*) (Martin et al., 1961). Avian predators include red-tailed hawks (*Buteo jamaicensis*), red shouldered hawks (*B. lineatus*), rough-legged hawks (*B. lagopus*), Cooper's hawks (*Accipiter cooperi*), goshawks (*A. gentilisi*), and golden eagles (*Aquila chrysaetos*), marsh hawks (*Circus cyaneus*), and crows (*Corvus brachyrhynchos*) (McAtee, 1935; Hagar, 1957; Gates, 1972; Trent and Rongstad, 1974; Johnson, 1978).

BEHAVIOR. Lord (1964) suggested that activity was not controlled by the onset of darkness. Activity was greatest in the summer months when nights were shortest. Lord speculated that the process of food assimilation might regulate the daily activity patterns of rabbits. Janes (1959) noted that activity was greatest at dawn and dusk, with increased activity on moonlit nights. Greatest activity occurred when air temperatures were between 0°F and 33°F. Rain apparently reduces activity. Janes (1959) stated that "activity increased as the percentage of ground covered by snow increased and as the abundance of food decreased." Lord (1961b) found that roadside activity was much greater in winter than in summer. Johnson and Hendrickson (1958) reported increased trap success, indicating increased activity, during or following rises in barometric pressure.

Exploratory males exhibit extensive chinning and paw-raking displays as described by Marsden and Holler (1964). Females also exhibit exploratory behavior when searching for nest sites (Marsden and Holler, 1964). Searching behavior by dominant males was also reported by Casteel (1966).

There are two general types of escape behavior, flushing and slinking. The flush is a "rapid, often zigzag movement to one of the established travel lanes, on which rabbits move at maximum speed to cover." When slinking towards cover the body remains close to the ground and the ears are laid back (Marsden and Holler, 1964).

Dog-like rolling in dusty areas (dusting) was also reported by Marsden and Holler (1964).

Marsden and Holler (1964) observed four distinct patterns of grooming: face grooming with front paws from eyes to muzzle, preceded by licking of paws; licking of the body and legs; scratching with the hind legs; and biting and cleaning of feet. Nursing females exhibited extended grooming sessions. Displacement activities of rapid face grooming and short feeding frenzies have also been noted (Marsden and Holler, 1964).

Male cottontails displayed alert posture, which involves raising the rump above the level of the shoulders and holding the ears upright, usually during confrontations with females or subordinate males (Marsden and Holler, 1964). Subordinate males displayed submissive posture (crouched position with ears reclined and tail held downward) when confronted by a dominant male. When males approached other males, the approaching rabbit assumed the alert posture. Sexually excited males were observed to dash past females when met with aggression by the females. During the dash, the male swung his rump in front of the female and urinated toward her. Rushes of a male directly at a female were also observed. Attempted mountings by males upon females were made without thrusting. Males, when interacting with females or subordinates, marked vegetation by rubbing it with the corner of the eye. Dominant males were also observed scratching and paw-raking with forepaws. This display occurred in the presence of other rival males (Marsden and Holler, 1964).

Female social behavior includes: threat posture consisting of a deep crouch position with chin up and ears laid back; boxing with approaching males, which entails striking out with forepaws from a raised threat position; charging in the threat position directly toward approaching males; jumping in response to a male's rush; and presentation of genitals to males by females in estrus (Marsden and Holler, 1964).

Three types of vocalizations have been reported, consisting of distress cries, squeals, and grunts. Distress cries are high-pitched screams emitted by frightened or injured rabbits which alert other rabbits. Squeals are sounded during copulation by either the female or the male. Nesting females emit grunts when their nest is approached by an intruder (Marsden and Holler, 1964).

Adult social interactions include those related to reproduction and to social hierarchies. Reproductive interactions consist of a sequence of patterns which precede and culminate in copulation. Initially, the male approaches the female and she turns, in a threat posture, to face the male (facing off). Immediately following the face-off, the male continues his advance towards the female. The female responds by boxing or charging the approaching male until he retreats. Females follow-up by chasing the retreating male. Males turn and dash at the passing female, urinating during the dash. After the dash, females shake their head, groom, and then retreat from the male. With more receptive females, jump sequences usually follow the male dash. In this chain of events, the male and female face-off, the male then rushes the female, the female jumps over the male, and finally they face-off again. When the female retreats from the male after a face-off, the male follows the female from behind, close enough to smell her hind quarters. A short reproductive chase of the estrous female by one or more males precedes copulation. During the copulatory act, the estrous female presents herself to the male, approaching from the rear. When mounting, the male clasps the female's flanks with his forelegs and initiates several rapid thrusts. Females then breakaway and are again pursued by the male (Marsden and Holler, 1964). Casteel (1966) reported successful copulatory chases lasting 10 sec to 7 min.

Dominant-subordinate interactions have been reported by Marsden and Holler (1964). Displays of aggression and submission usually indicate dominance. Subordinates move away from dominants, or crouch in a submissive posture. Dominant males often charge subordinates, forcing them to retreat (dislodgement). The dominant male then sniffs the vacated area. Pursuit does not follow dislodgement. Dislodgement by females is essentially the same as for males. Aggressive chases differ from dislodgement in that dominant animals aggressively pursue the subordinate. Male-male chases are of longer duration than female-female chases. Fighting does occur although it is not a part of normal social activity. Biting and kicking and striking with the feet have been observed, but extensive fighting does not develop because one animal always gives ground quickly (Marsden and Holler, 1964).

Male hierarchies prevent reproductive fighting. Nearly all male aggression is initiated by dominant males. Challenges for social status have only been observed between the top two males.

Dominant males copulate with the majority of females (Marsden and Holler, 1964).

Interspecific aggressive behavior was observed between introduced *S. floridanus* and native brush rabbits (*S. bachmani*) in Oregon (Chapman and Verts, 1969). One such aggressive encounter within an enclosure resulted in the death of the brush rabbit.

Chapman and Trethewey (1972*b*) studied the responses to traps by introduced eastern cottontails in the Willamette Valley of Oregon. They found that females were more frequently recaptured than males, and that juveniles were more frequently recaptured than adults. All sex and age groups of cottontails were most easily captured in January. A positive correlation was found between cottontail captures and barometric pressure. As temperatures became colder, individuals were trapped more frequently.

Kirkpatrick (1956) observed coprophagy in *S. floridanus*. Soft pellets were eaten directly from the anus before they touched the ground, and was limited to two or three pellets at a time.

GENETICS. The eastern cottontail has a diploid chromosome number of 42, with six metacentric or nearly metacentric pairs, 11 submetacentric pairs, and three acrocentric pairs of autosomes (Holden and Eabry, 1970). *S. floridanus* differs from *S. transitionalis* in that the latter has 52 chromosomes. The Y chromosome is acrocentric and is the smallest of the complement, while the X chromosome is a medium sized submetacentric. Four pairs of submetacentric chromosomes have secondary constrictions in the long arms and two pairs of acrocentric chromosomes have prominent satellites on the short arms (Holden and Eabry, 1970).

Chapman and Morgan (1973) examined the blood sera of several species and subspecies of *Sylvilagus* by electrophoresis, including 277 individuals of *S. floridanus* (42 *S. f. alacer*, 18 *S. f. mearnsi*, 5 *S. f. chapmani*, and 212 intergrades between various subspecies). All of the *S. floridanus* examined had unique protein systems, with intergrades of *S. floridanus* showing more polymorphism than all others they examined, including *S. audubonii* and *S. transitionalis*. The polymorphism found in the intergrade *S. floridanus* included varient tranferrins. Detailed electrophenograms and schematic drawings were presented for several members of the genus *Sylvilagus*, including four subspecies of *S. floridanus*. Johnson (1968) also examined blood sera from 17 *S. floridanus* and several other *Sylvilagus*, and reported that they differed significantly from *Brachylagus idahoensis*.

REMARKS. The eastern cottontail is an important game animal and provides millions of hours of recreational sport each year. This species has been more intensively studied than any other rabbit. These studies include numerous M.S. and Ph.D. theses as well as hundreds of Federal Aid to Wildlife Restoration reports (Pittman/Robertson). Because of page limitations here, and the nature of many of the reports, we have not cited most. Contribution Number 947-AEL, Center for Environmental and Estuarine Studies, University of Maryland.

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